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A study of the vertical distribution of upper mesopelagic animals in the Monterey Submarine Canyon, California

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A STUDY OF THE VERTICAL DISTRIBUTION OF UPPER MESOPELAGIC ANIMALS IN THE MONTEREY SUBMARINE CANYON, CALIFORNIA

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ABSTRACT

A STUDY OF THE VERTICAL DISTRIBUTION OF UPPER MESOPELAGIC ANIMALS IN THE MONTEREY SUBMARINE CANYON, CALIFORNIA

by Lisa Smith-Beasley

Temporal and vertical distribution patterns of all identifiable taxa were analyzed from 54 midwater discrete-depth trawl samples collected in September, 1985 between 140 and 500 m in the Monterey Submarine Canyon, California. Over 125 species from seven phyla were identified. Crustaceans were the dominant taxa, comprised primarily of euphausiids. Fishes were dominated by myctophids. There were at least three distribution patterns. The first included predominantly epipelagic organisms which migrated to deeper waters in the daytime. The second included deeper mesopelagic migrators which exhibited various diel vertical patterns. The third category, mesopelagic residents, stayed at depth. Qualitative comparisons with preliminary data from concurrent submersible dives revealed a much higher proportion of gelatinous fauna and fewer crustaceans in the submersible records. A general conclusion is that midwater trawls are suitable for systematic, medium-scale studies, while submersibles are more effective in microscale studies, especially those of fragile gelatinous taxa.

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Introduction

The Monterey Submarine Canyon is one of the largest underwater canyons on the west coast of North America (Greene, 1977; Allen, 1982) (Figure 1). Starting offshore southwest of the mouth of Elkhorn Slough, it meanders generally southwest for about 100 km before opening to the head of the Monterey Deep-Sea Fan at a depth of approximately 3,000 m. It reaches a maximum vertical relief of 1,500 m and width of 20 km (Allen, 1982). This juxtaposition of nearshore and canyon waters gives rise to a local fauna characterized by a combination of coastal, oceanic and deep-sea organisms (Barham, 1957; Bolin and Abbott, 1963; Kukowski, 1972).

Despite years of deep-sea research in Monterey Bay, there has been no detailed collective examination of the vertical distribution of its deep (below 150 m) fauna. Parts of the mesopelagic fish fauna were well studied, including Cyclothone signata (Aughtry, 1953), Stenobrachius leucopsarus (Fast, 1960), Melanostigma pammelas (Yarberry, 1965), Lycodapus mandibularis (Anderson, 1977), and certain fish collections (Kukowski, 1972; Anderson, Cailliet, and Antrim, 1979). Investigation of the sonic scattering layers (Barham, 1957) included discussion of the dominant fishes and invertebrates, but cephalopods (Anderson, 1978) have been the only mesopelagic invertebrate group examined individually.

In the past, only indirect methods have been available to study deep-sea animals. These include trawls, hook-and-line, predator stomach contents analysis, incidental commercial catches, accidental entanglements, and strandings (Marshall, 1954; Anderson, Cailliet, and Antrim, 1979). These have provided a broad picture of the deep-sea fauna, but the potential for new information from these techniques may be diminishing (Carter Hanson and Earle, 1987). For new insights, other techniques must be applied to the deep pelagic zones.

Technological progress has brought new research tools in the form of manned and unmanned submersibles. Although still mostly qualitative, in situ observations, collections, and experiments from these submersibles add new depth to the understanding of the deep-sea, including the lower pelagic zones.

Trawls and submersibles have been used to supplement or verify each other. Several studies used both techniques to explore fine-scale resolution of the deep scattering layer (Barham, 1963; Davies and Barham, 1969; Clarke, 1970; Pickwell et al., 1970). Also, submersible-based research has used trawls taken in the same area to get voucher specimens and verify identifications (Mackie and Mills, 1983; Alldredge et al., 1984; Mackie, 1985).

In these cases, comparisons between the trawl and submersible data were limited, with one technique used as a supplement to the other. Opportunities for detailed, concurrent comparisons in the deep pelagic zones have been restricted. Advantages and biases of each method, some obvious and others not, have been assumed and theorized, but often these assumptions have not been tested.

The first research submersible to study the Monterey Canyon mesopelagic fauna was the R/S Deep Rover in the fall of 1985. This single-pilot autonomous submersible is portable, low-cost, highly maneuverable, and user-friendly (Carter Hanson and Earle, 1987). The goals of the DEEP ROVER 1985 Canyon expedition included: 1) in situ observations of the abundance, distribution, and behavior of mesopelagic organisms; 2) demonstration of the feasibility of conducting midwater research with a single-place, untethered submersible; 3) research on bioluminescence; and 4) documentation of the occurrence and behavior of the midwater fauna with video (B. Robison, pers. comm.).

The 1985 DEEP ROVER expedition also provided the opportunity for concurrent sampling of the upper mesopelagic zone by trawl and submersible surveys (Figure 1). The goals of the trawl survey included: 1) obtaining a quantitative description of the diel vertical distribution of a broad array of upper mesopelagic fauna of the Monterey Submarine Canyon; 2) examination of the results with preliminary data from the R/S DEEP ROVER to develop a better understanding of the fauna; and 3) comparison of these concurrent samples to explore the best uses and limitations of each method in the study of the deep pelagic fauna. Together they provide a more comprehensive view of the rich and diverse fauna of the Canyon than previously possible.

Materials and Methods

Trawl Survey

Trawl samples used in this study were collected from the R/V CAYUSE in a series of discrete-depth, midwater hauls on 3-11 September 1985. This was during the relatively calm and warm oceanic period (Bolin and Abbott, 1963; Breaker and Broenkow, 1989), which facilitated the concurrent dives of the R/S DEEP ROVER. A modified 1.8 m (6 ft.) Rectangular Midwater Trawl (RMT) (Davies and Barham, 1969) with 4 mm mesh and a 0.505 mm cod end used, and was equipped with a timed double-release mechanism to open and close the net when sampling (Davies and Barham, 1969). To minimize damage to specimens, the soft cod end was fitted with an outer terylene bag (Baker et al., 1973).

This study targeted depths between 140 and 500 m, known as the upper mesopelagic zone (Hedgpeth, 1957; Pearcy et al., 1977), to complement the depths investigated by the R/S DEEP ROVER. There were four trawls each day and three each night. The trawls were 2-2.5 hrs apart, with a rest period for the collecting team sometime between 0400 and 0700. While towing, the ship maintained a trawling speed of about two knots. Once the net was retrieved, the precise duration and depth of each trawl were determined by a Benthos time-depth recorder (TDR), model number 1170-730m. Bottom depth and deep scattering layer (DSL) information were recorded from a precision depth recorder (PDR), and showed that most samples were taken at least 100 m above the bottom (Appendix 1).

Six trawls were excluded from analysis. Four of these had questionable data on the duration or depth of the sample. In addition, two samples were used by the DEEP ROVER researchers for voucher specimens. This resulted in 54 usable trawls ranging in depth from 140 to 495 m (Appendix 1).

Once on board, the bulk of each trawl was rough-sorted into three general categories of fishes, crustaceans, and gelatinous organisms. Any healthy specimens were identified, counted, and logged; aquarists from the Monterey Bay Aquarium then attempted to keep them alive. Everything else was preserved immediately in 10% buffered formalin. Samples were later rinsed in fresh water and transferred to 40. isopropyl alcohol, then sorted, identified to the lowest possible taxon, and enumerated. Some cnidarians, because of damage by the trawl, could only be noted as present or absent.

To facilitate enumeration. the larger crustacean samples (over one liter in volume), were aliquoted and four 1/16 portions were sorted. A preliminary analysis showed at least 95 percent similarity in species composition between 4/16 of the sample and the entire sample. A few samples which totalled over 4 liters (and thus containing 15,000 to 53,000 animals) were aliquoted, but only two 1/16 portions were analyzed. The 90% similarity of these samples to the whole exceeded the 80% standards deemed sufficient by other studies (Youngbluth, 1975).

All data were converted to number per 10 minutes of trawling since the amount of time the net was open varied between 13 to 33 minutes. Ten minutes encompassed approximately 2000 m^3 of water, but no flowmeter was available. Based on a 0630 sunrise and 1930 sunset at that time of year, the data were further divided into 31 day and 24 night samples. The trawl data were then arbitrarily grouped for analysis by depth into 100-199, 200-299, 300-399, and 400-499 m increments. This resulted in five to nine trawls per interval.

The cumulative number of species taken by successive trawls was calculated and graphed. The resulting cumulative species curve was used to determine if sufficient samples were collected to adequately characterize the species composition at each depth and time-of-day category (Hurtubia, 1973).

Distributions of all taxa were examined for patterns over time and depth intervals. First, all species or taxonomic groups were categorized by their abundance within each interval: either a single occurrence (1), infrequent (IF: in 60% of the tows or less), common (C: in more than 60% of the tows), abundant (A: interval mean = 10-99 per 10 minutes), superabundant (S: interval mean $>$ 10 but $\leq$ 100 per 10 minutes, and SS: interval mean $>$ 100 per 10 minutes).

Variations in species between the depth and time intervals were examined. The dominant species were graphed as mean number ± standard error. Day versus night depth variations in species distributions were considered in relation to known diel vertical movements.

The fauna was also examined for trends over depth and time, grouped as invertebrates or fishes. Regression analyses were used to test for relationships of number of species versus depth and diversity (measured as the Shannon-Weiner index H') versus depth. A percent similarity index (PSI) (Krebs,1989) was calculated between depth and time intervals, and both high and low similarities were examined. A similarity of 80% was used as an arbitrary level of significance (Youngbluth, 1975). For both indices, invertebrates were examined without the euphausiid Euphausia pacifica. This species could occur in extremely large numbers, and biased any proportional computation. The impact of dominant species and groups on these indices was also examined.

Submersible Survey

The R/S DEEP ROVER surveys began on 18 August 1985 and continued for one month. Of the 50 dives averaging four hours each (Carter Hanson and Earle, 1987), 12 were suitable for sampling comparisons. Data were collected by Dr. Bruce Robison and included continuous verbal logs of dives, video tapes of notable events, and collections by suction sampler. For this study, the transcripts were reviewed for pelagic data. One dive was interrupted by a return to the surface, and was counted as two dives. Sections examining cliff faces or the benthos were excluded. Occasionally the log indicated animals following the submersible up or down, and these data were also excluded. The shallowest recorded occurrences of taxa or morphotype were enumerated and when in common to both methods, were compared. The frequency of occurrence of taxon (proportion of dives each taxa was reported) was compiled. The ten most common taxa were ranked by frequency and abundance (how many times a taxon was reported in each dive). Similar rankings, based on occurrence in intervals and overall abundance of trawl samples were compiled for comparison.

Results

Not all animals from trawls were identifiable to species level. Despite that limitation, at least 125 species distributed among seven phyla were identified in the collections. Almost all of the common species showed highly variable abundances, with large standard errors in most intervals (Figs. 3-9).

The cumulative species curve for each of the eight time/depth intervals started to level at approximately four samples, although the number of species varied by interval (Figure 2). Additions after the fourth replicate were the most uncommon species. The incremental increase per sample decreased after the sixth collection. However, additional species continued to appear through at least the eighth trawl.

Upper Mesopelagic Species

Cnidaria

Despite the considerable damage caused by the trawl, 14 species of cnidarians, representing two orders and seven suborders, were recorded. Most were collected from below 300 m (Table 1).

Medusae

No strong diel shifts in abundances of medusae were apparent, though temporal variations occurred (Table 1). Some species, including Euphysa spp., Ptychogena spp., and Aegina citrea, decreased in number by night, at least at the upper portions of their range. At night, other species became more numerous, including Tiaranna spp., Colobonema sericeum, and Periphylla periphylla and were found shallower. The distribution of a few, such as Atolla wyvillei remained relatively unchanged over time.

The medusae were dominated by a large unidentified leptomedusan (Figure 3A). The loss of most body structures precluded specific identification. The abundance of leptomedusae increased below 200 m by night, mostly at the 300 m interval.

Siphonophora

Two suborders of siphonophores were identifiable in this study: Solitary calycophora and colonial physonectae (Table 1). Calycophorans were abundant in the deeper samples (Figure 3B), with some variation between day and night. Pieces of physonect siphonophores were noted irregularly (Table 1).

Ctenophora

Only two species of ctenophore were collected (Table 1). Hormiphora (=Euplokamis) californiensis was most numerous (Figure 3C). It was present at all depths sampled, but numbers steadily decreased with depth. There were few differences between day and night abundances. The other ctenophore, Beroe spp., occurred infrequently (Table 1).

Mollusca

Three species of pteropods and one heteropod were collected (Table 2). Clione limacina was common at all depths and times of day. The other thecosome, Corolla spectabilis, was most common below 200 m by day and above that by night. The gymnosome Clio pyramidata and the predatory heteropod Carinaria japonica were infrequent at almost all depths (Table 2).

At least five squids and two octopods were collected (Table 2). In most cases these were larvae or juveniles. Most frequent were juvenile Gonatus spp., which were most common below 400 m by day and between 200-299 by night. This and several other squid species were more numerous in shallower intervals at night (Table 2). The octopods, Octopus spp. and Japatella heathi, were especially small, less than two cm.

Annelida

Three polychaetes were collected, of which Tomopteris spp. was most numerous (Table 3). Its abundance was highly variable within and between depth and time intervals. Two other species, Poeobius meseres, and postlarval Aphrodita spp., were infrequent, and usually found below 300 m (Table 3).

Crustacea

Crustaceans were the dominant class in the samples. Only fishes showed similar diversity, but no other group had comparable abundance.

Ostracoda

One small white ostracod was collected but not identified (Table 4). It was infrequent above 400 m at all times, but dropped in numbers below 400 m at night.

Copepoda

Several taxa of copepods were collected, but only one, Gaussia princeps, was identified to species (Table 4). Gaussia princeps decreased in numbers at night. Most copepods were collected by day in the lower intervals, especially below 400 m (Figure 4A). By night, they were widely distributed among depth intervals.

Mysidacea

Three mysids were collected, two of which were abundant (Table 4). Most abundant was the smaller Boreomysis californica, most frequent below 400 m (Figure 4B). Holmesiella anomala had a slightly shallower distribution (Figure 4C); it was most abundant below 200 m. This species has not previously been reported in Monterey Bay. The few Eucopia spp. were from below 300 m.

Amphipoda

Amphipods were the most diverse order of crustaceans, with two suborders, 17 families, and at least 24 species (Table 5). Of these, the hyperiid genera Lycaea and Mimonectes, species Primno brevidens; gammarid genera Cleonardo, Valettiopsis, and Hyperiopsis, species Paracallisoma alberti and Parandania boecki were previously unreported in Monterey Bay.

The distribution of hyperiid amphipods was highly variable (Table 5). Paraphronima spp., the most abundant genus, was collected in its highest numbers above 200 m by day (Figure 5A). The members of the common families Hyperiidae and Phrominidae showed little change with time. Other groups such as the Phrosinidae varied without a distinct pattern.

Orchomene spp. was the most numerous gammarid (Figure 5B). Most other gammarids only appeared by day below 400 m (Table 5).

Euphausiacea

The first- or second-ranking, dominant species at most depths was Euphausia pacifica (Table 6). This species was most abundant above 200 m by day, and below 400 m at night (Figure 6A). Its distribution was extremely variable, especially above 200 m (Figure 6A). The highest concentrations were part of the deep scattering layer. Trawl number 29, from an intense daytime deep scattering layer at 210 m, collected over 53,000 euphausiids in 28 minutes.

The other common euphausiids, Nematoscelis difficilis and Thysanoessa spinifera, became more abundant in the trawl collections at night (Figure 6B,C). The infrequent Nematobrachion flexipes was collected only twice, at night between 200 and 400 m (Table 6).

Decapoda

There were diel changes in abundance of both peneids, Sergestes similis and Gennadas propinquus (Table 6). This was most distinct in the case of S. similis, which was concentrated between 200-400 m by day, and above 200 m at night (Figure 7A).

The distribution of the carid Pasiphaea pacifica resembled that of S. similis, but in lower numbers (Figure 7B). The other carids were infrequent, but were also more common in shallower water at night (Table 6).

Larvae of benthic decapod crustaceans, usually crabs, were common at most depths (Table 6). They became infrequent below 300 m at night.

Chaetognatha

Chaetognaths, primarily Sagitta spp., formed a significant portion of the fauna below 300 m (Figure 8A). There were no clear variations in abundance over time, although there was an increase in numbers at night.

Thaliacea

Four genera of salps were collected (Table 7). Salpa fusiformis was most common, although it was still infrequent in these samples. Thalia democratica was next in abundance, followed by Iasis zonaria. Trawl damage prevented identification of most other salpids except for a few Cyclosalpa spp.

Dolioletta gegenbauri was the only doliolid collected (Figure 8B). Most of the individuals collected were in the resting form of the "nurse" stage (Berner, 1957) of its life history (Table 7). There was a drop in its numbers below 400 m.

Fishes

Three classes, 28 families, and 49 fish species were collected (Tables 8-10). Fifteen of these species from 13 families were single occurrences within a depth interval. Only four species were abundant (Figure 9). Fourteen additional species were common in at least one interval (Tables 9, 10).

Large fishes

Only seven large (> 0.5 m TL) fishes were collected (Table 8). Each was caught singly below 200 m. These included a Lampetra tridentata, an Icosteus aenigmaticus, and four sharks. All the sharks: Parmaturus xaniurus, two Apristurus brunneus, and Somniosus pacificus were juveniles.

Larval fishes

Fourteen fish families including 17 species were represented only by larvae or postlarvae (Table 9). Flatfishes were most numerous, usually Errex zachirus, Citharichthys stigmaeus, C. sordidus, and Eopsetta exilis. Most flatfishes were more frequent above 200 m at night. An exception was Microstomus pacificus, which was only caught below 200 m.

Bathylagidae

The bathylagid Leuroglossus stilbius was numerous throughout the sampled range. It was most abundant below 300 m by day and above that depth by night (Figure 9A). The other two bathylagids collected, Bathylagus ochotensis and B. wesethi, were only found below 400 m by day.

Gonostomatidae

Gonostomatids were represented by four species of Cyclothone (Table 10), but only C. signata was abundant. It was most numerous below 300 m (Figure 9B), and often the dominant fish. There was little diel variation in abundance in any members of this family.

The congeners of C. signata were much less frequently encountered (Table 10). Next in abundance were C. pseudopallida, C. pacifica, and finally C. acclindens. All were most numerous below 400 m.

Sternoptychidae

At least 3 genera and 4 species of sternoptychids were collected below 300 m in this study (Table 10). Since most specimens were transferred to the Monterey Bay Aquarium before identification, there may have been more species of Sternoptyx and Argyropelecus collected than recorded.

Bathypelagic fishes

Some fishes were found only below 300 m by day, but were shallower and more numerous at night (Table 10). Chauliodus macouni was caught primarily in the deeper trawls. Only larvae were collected above 300 m. Idiacanthus antrostomus was only collected from below 300 m, and was most common below 400 m by night. Below 400 m small Tactostoma macropus was collected at night, and Scopelengys tristis by day.

Myctophidae

Seven species of myctophids were divided among six genera (Table 10). It was both the most speciose and abundant fish family above 300 m, and second only to the Gonostomatidae below that depth. Stenobrachius leucopsarus comprised the bulk of the myctophids (Table 10). Its was distributed through the sampled depth range, but its abundance peaked between 200 and 300 m but most were below 200 m by day and above 300 m at night (Figure 9C).

Three other myctophids were frequent at deeper intervals (Table 10). Lampanyctus ritteri was common below 300 m by day and spread throughout the sampled range by night. Next in abundance were Tarletonbeania crenularis and Protomyctophum crockeri. Both were well represented by larvae and adults, especially T. crenularis. By day, the larvae of P. crockeri were found well above adults, within the 100 m interval.

Other myctophids were infrequent, even by night (Table 10). Lampanyctus regalis occurred only as solitary specimens, though they were more frequent at night. Diaphus theta and Diogenichthys atlanticus were infrequently collected.

Zoarcidae

Of the two zoarcids collected, Lycodapus mandibularis was most common (Table 10). It was most numerous below 400 m, but became more common up to 200 m at night (Figure 9D). Melanostigma pammelas was collected below 400 m by day and up to 300 m at night.

Cyclopteridae

Two species of cyclopterids (liparids) were collected in this study (Table 10). Nectoliparis pelagicus was found below 300 m by day and in all intervals at night. A few Lipariscus nanus were collected below 300 m.

Upper Mesopelagic Groups

Invertebrates dominated the collection, with a few species being very abundant. Crustaceans, including euphausiids, decapod shrimps, and mysids in turn dominated the invertebrate fauna. They comprised 50% to 97% of the total specimens collected. Fishes were much less abundant, but were dominated by myctophids above 300 m and by gonostomatids below.

There was a significant ($p < 0.01$) increase in the total number of invertebrate (day $t = 0.827$, night $t = 0.732$) and fish (day $t = 0.881$, night $t = 0.767$) species with increased depth. The mean number of invertebrate species went from 20 between 100-199 m to 40 between 400-499 m by day, and from 23 to 34 species in the same intervals by night (Figure 10A). At the same intervals, the mean number of fish species went from 3 to 16 by day, and from 8 to 15 species by night (Figure 10B).

Some trends in the percent similarity index (PSI) were apparent, though few inter-depth similarities exceeded 80% (Table 11). When Euphausia pacifica was included, it usually overwhelmed any other relationships (Table 11A), but there were patterns to the subdominant fauna.

Without E. pacifica, the intra-depth similarity was 65% or above (Table 11B, C). For invertebrates, there were also two areas of higher inter-depth similarity. The first was the 200-299 m day interval versus nighttime depths between 100-299 m. A second was below 400 m by night versus 300-499 m by day (Figure 11B). Other relatively high similarities were between the 300-399 day interval versus any night interval.

Fishes showed a similar pattern, especially below 300 m (Table 11C). In the shallower intervals, it was the 200-299 night interval that was similar to between 100-299 m by day.

The low inter-depth similarities could also be used to separate groups. For both invertebrates and fishes, the lowest similarity indices were between the 100-199 m day interval versus below 300 m by night and below 400 m by day versus above 300 m by night (Table 11).

The patterns of diversity (H') varied between invertebrates (not including E. pacifica) and fishes (Figure 11). There was no significant relationship with increasing depth and invertebrate diversity by day ($r = 0.208$). However, diversity increased significantly ($p < 0.01$) with depth for daytime invertebrates ($r = 0.660$), and fishes by day ($r = 0.668$), and night ($r = 0.785$).

Submersible Observations

Although the data from the DEEP ROVER survey logs are only preliminary, there were trends among taxa. The submersible recorded at least 55 taxa from 8 phyla. Of these, foraminiferans were reported exclusively by the submersible.

Significantly more gelatinous taxa were recorded in situ. At least 13 taxa of cnidarians were noted, comparing well to the 14 from trawling. However, at least eight ctenophore species were observed, of which only two were recognizable in the trawl.

However, other taxa were much less commonly recorded by the submersible. Far fewer crustacean and fish taxa were recorded. Although 24 species of amphipods were collected in trawls, members of this group were only noted in 4 dive transcripts. Fishes were regularly reported, but only 15 types were identified to family or species, in comparison to the 49 species collected by trawls.

When the shallowest recorded occurrences of taxa within this study were compared, there were some significant differences (Table 12). Fourteen taxa, including nine types of fishes, were collected by trawl at least 50 m shallower than the first submersible record. Two fishes, Merluccius productus and Melanostigma pammelas were caught between 15 and 50 m deeper by trawls. Eleven taxa, including four fishes, were recorded within ± 15 m by each method. Although no pattern seems apparent in the shallowest occurrences of cnidarians and ctenophores, this comparison excluded a large number of different types described from the submersible yet absent from trawl samples.

Five of the 10 most frequently occurring taxa, including euphausiids, decapod shrimps, Stenobrachius leucopsarus, and Leuroglossus stilbius, were common to both methods, although in different order ranks (Table 13). The top ranking species within trawl samples included calycophorid siphonophores, chaetognaths, doliolids, and copepods. Physonect siphonophores, ctenophores and one fish species, M. productus, were abundant only in situ.

Also notable in the submersible observations was the patchy distribution of many species, both vertically and horizontally. Schools or aggregations of M. productus, squid, and euphausiids were reported, though apparently some were attracted to the submersible. Some of the euphausiid swarms were undergoing mass molts. Various fishes were seen associated with the siphonophore Apolemia.

Discussion

Both the submersible log transcripts and the high standard errors from trawl samples indicated that animals were patchily distributed in this study. These nonrandom horizontal and vertical patches are not uncommon (McGowan and Fraundorf, 1966; Harrisson, 1967). Schools or narrow layers of copepods (Alldredge et al., 1984; Vinogradov et al., 1985), euphausiids (Hamner et al., 1983; Mackie and Mills, 1983), and fishes (Pearcy, 1964; Barham, 1970; Robison, 1972) have been observed. Variability would be even greater when the species were known migrators as well (Pearcy, 1964; Barham, 1970; DeWitt, 1972; Robison, 1972; Hamner et al., 1983; Mackie and Mills, 1983; Alldredge et al., 1984).

Despite this variability, many of the upper mesopelagic animals in this study showed indications of diel vertical migration. This is a consistent pattern of daytime retreat and nighttime rising with low variability in abundance (Robison, 1972; Marshall, 1979; Cailliet and Ebeling, 1990). Other longer-term studies confirm these indications for many of the species collected in this study. Patterns varied by taxa, but could be divided into three characteristic groups: 1) epipelagic migrators; 2) deep pelagic migrators; and 3) mesopelagic residents. These are groups implicitly or explicitly recognized in many pelagic studies (e.g. Brinton, 1967; Paxton, 1967; Ebeling et al., 1970; Robison, 1972; Omori, 1974; Pearcy et al., 1977; Willis and Pearcy, 1982; and Mackie, 1985), but the upper mesopelagic zone is where they overlap.

Upper Mesopelagic Species

Epipelagic Migrators

The epipelagic migrators were collected above 200 m by day and were less abundant at night. Although these epipelagic species would be most abundant between the surface and 100-200 m, a residue continuing into the mesopelagic zone had a significant impact on the species composition and diversity at these depths. This was especially true with the euphausiids, hyperiid families Hyperiidae and Phrosinidae (Hurley, 1956; Marshall, 1979) and larval fishes (Harrisson, 1967; Ebeling et al., 1970; Loeb, Smith, and Moser, 1975).

The most abundant taxon in this study was the epipelagic euphausiids, mostly Euphausia pacifica. Although most E. pacifica are found above 200 m, a substantial number can be found as deep as 1000 m (Boden, Johnson, and Brinton, 1955; Brinton, 1962; Cailliet and Ebeling, 1990). In this study, they dominated the upper mesopelagic zone at most times, but could show extreme variations in abundance.

Swarming of E. pacifica may have been responsible for some of the variation in abundance in this study. Daytime surface swarms occur off California from July through September (Boden et al., 1955; Brinton, 1962; Smith and Adams, 1988; Harvey, 1989). However, the physical and biological factors proposed to create surface swarms (Endo, 1984; Smith and Adams, 1988) would not necessarily apply to midwater conditions. Swarms may be part of the deep scattering layers (Barham, 1963), or are independent and nonmigratory (Mackie and Mills, 1983). They may have aggregated to undergo mass molts observed by the R/S DEEP ROVER. Further information on subsurface swarming may come as serendipitous discoveries, as were many previous reports.

Some epipelagic species lack sufficient research to determine to what extent they migrate. Corolla spectabilis (McGowan, 1968) showed signs of vertical migration, which is supported by its behavior in the Florida Current (van der Spoel, 1976). Local thaliaceans also show some indication of migration, though their very patchy distribution prevents confirmation of migration (Berner, 1957). However, Salpa aspera, the Atlantic congener of the local S. fusiformis, migrates up to 800 m (Wiebe et al., 1979). The presence of high numbers of Dolioletta gegenbauri in the nurse phase is not understood.

Deep Pelagic Migrators

A majority of species in this study were migrators from the mesopelagic and bathypelagic zones. They usually inhabit these depths by day, and move to shallower zones at night.

Many of the common taxa were found by day in the mesopelagic zone and near surface at night. The diel vertical migrations of these species is confirmed by other studies. Locally, the movements of Euphysa spp. and Clione limacina were similar to, though deeper than, migrations reported off British Colombia (Mackie, 1985). Squids (Roper and Young, 1975; Anderson, 1978), mysids (Kathrnan et al., 1986), and decapod shrimps (Omori, 1974; Pearcy et al., 1977), are known migrators as implied in this study. Sergestes similis and Pasiphaea pacifica probably follow the migrations of their prey (Omori, 1974). Although Holmesiella anomala migrate, (Kathman et al., 1986), the high variability of this collection obscured any pattern.

The most detailed studies of migrations in the eastern Pacific Ocean have been on fishes, and several dominant species in this study are known migrators. This includes all the bathylagids collected (Miller and Lea, 1972; Willis and Pearcy, 1982; Cailliet and Ebeling, 1990), the myctophids (Wisner, 1974; Willis and Pearcy, 1982), and Lycodapus mandibularis (Anderson, 1977).

Although myctophids are active migrators, a substantial portion of the population remained within the range of this study at all times. They spread throughout the upper mesopelagic zone at night, considerably enhancing diversity. The dominant myctophid, Stenobrachius leucopsarus, is known to form shoals or aggregations (Pearcy, 1964; Barham, 1970) which may explain its sometimes high variability in this study.

Many amphipods represented in this study are concentrated between 200-600 m by day and higher at night (Brusca, 1967). These species, including the hyperiid Vibilia and gammarid Cyphocaris anonyx, spread upwards by night and are found throughout their vertical range at night. Others combine ontogenic as well as daily migrations (locally, Phronima spp. and Primno macropa). Many species are also associated with gelatinous fauna (Laval, 1980; Harbison, 1983), and could be distributed according to the movements of the host.

Some pelagic species collected in this study are closely allied to the deep scattering layer. These include siphonphores (Barham, 1963; 1966), amphipods (Davies and Barham, 1969), Euphausia pacifica, Sergestes similis, several myctophid species (Barham, 1957), and possibly Cataetyx rubrirostris (Gibbs, 1991).

Most of the larval bathypelagic or mesopelagic fishes were collected shallower than the adults. The difference can be up to several hundred meters, depending on species (Fitch and Lavenberg, 1968; Willis and Pearcy, 1982; Eschmeyer et al., 1983). Young Chauliodus macouni, Idiacanthus antrostomus, and Tactostoma macropus are known to migrate to near the surface (Fitch and Lavenberg, 1968; Pearcy et al., 1977; Willis and Pearcy, 1982). In this study, they also spread through the upper mesopelagic zone. Unlike the adults, the young sharks collected in this study, Parmaturus xaniurus, Apristurus brunneus, and Somniosus pacificus are often collected well off the bottom (Lee, 1969; Miller and Lea, 1972; Eschmeyer, Herald, and Hammann, 1972; Hart, 1973; Ebert, Compagno, and Natanson, 1987).

Migrations of other taxa can be more complex. Copepod migrations are influenced by many factors, including life history stage, food availability, distance from shore, and predation (Alldredge et al., 1984; Huntley 1985; Vuorinen, 1987). Comprehensive taxonomic and life history studies would be needed to understand their distribution. The migrations of Leuroglossus stilbius vary by location and the type and abundance of food (Cailliet and Ebeling, 1990). Other species in this study are known to undergo reverse migrations, including the hyperiid Primno macropa and gammarids (Brusca, 1967). This may explain their absence in the shallower intervals by night.

Mesopelagic Residents

Although nonmigratory, mesopelagic residents may show weak vertical movement by night (DeWitt, 1972; Kobayashi, 1973; Pearcy et al., 1977). Only one species, Hormiphora californiensis, was most common in the shallower intervals. Since the taxonomy of this genus has only recently been clarified

(Mills, 1987), diel variations reported in British Columbia (Mackie, 1985) may be interspecific. Other invertebrates include the juvenile octopods (Roper and Young, 1975; Anderson, 1978), and possibly annelids, although there has been little research on the life history of pelagic worms. Poeobius meseres is one of the few annelids that has been studied recently (L. Uttal-Cook, pers. comm.). Gammarid amphipod taxonomy is complex enough to aggravate the problems of researching them. Systematic study could determine if more invertebrate taxa do migrate.

The dominant fishes of the the lower mesopelagic and bathypelagic zones are the nonmigratory gonostomatids (Mukhacheva, 1966; Kobayashi, 1973; Willis and Pearcy, 1982). In this study, they also dominated the upper mesopelagic fish fauna.

Most of the other resident fishes were also collected at the top of their ranges, including sternoptychids and Scopelengys tristis, (Fitch and Lavenberg, 1968; Ebeling et al., 1970; Miller and Lea, 1972), and liparids, (Stein, 1978). However, Melanostigma pammelas was collected shallower than previously reported in Monterey Bay (McAllister and Rees, 1964).

Upper Mesopelagic Groups

In this depth range of this study, the number of species increased with depth. This is due to the characteristics of this zone, which is the shallowest depth many mesopelagic species are found, and the very deepest vertical range of epipelagic species. The diversity and abundance of fauna from both the epipelagic and mesopelagic zones are attenuated at this depth, especially above 100 to 200 m. This is most pronounced for fishes above 200 m. At all time intervals, the increase in species with depth came from the addition of mesopelagic species. The mean number of species per trawl increases by night because these mesopelagic animals became more common as the move into shallower waters . Relatively few new species arrived in this zone from below 500 m by night.

The subdominant fauna, all species excluding Euphausia pacifica, appeared to occur in depth zones. The highest similarities for both fishes and subdominant invertebrates were in the deepest intervals, from below 300 to 400 m. Abundant residents there included chaetognaths, copepods and gonostomatids. By night, some members of the migratory species remained behind with the residents below 400 m. These species, including mysids, decapod shrimps, myctophids, and Lycodapus mandibularis, accounted for the high similarity between day and night. These species were not caught between 100-300 m, and may have passed through this interval on their way to the surface at night.

The low similarity of fish and invertebrate fauna taken above 200 m by day versus that below 300 m at night came from different faunal influences. With invertebrates, there were several epipelagic species, primarily amphipods and Hormiphora californiensis, dominating the fauna during daytime. However, they were much less abundant than the deeper migrators that joined them at night. For fishes, there were very few individuals of any type above 200 m by day, with only Leuroglossus stilbius being common. The nighttime arrival of mesopelagic species at that depth created a diverse and abundant assemblage.

These patterns of migrating, spreading, and residencies emphasized the importance of faunal input from adjacent depths, whether epipelagic, mesopelagic, or bathypelagic. A portion of the population of many species were above or below the typical ranges of that species. There was a change in proportions of fauna at approximately 300 m, above which epipelagic species dominated, below that the fauna had a more truly mesopelagic composition. However, the dominant influences are different for invertebrates and fishes. The numerically dominant invertebrates are epipelagic, primarily euphausiids and thaliaceans. Also, the epipelagic amphipods add considerable diversity to the invertebrate collection. The fish fauna is dominated by mesopelagic and bathypelagic species, including myctophids and gonostomatids.

Few migrations were simple or complete. At night, species can spread upwards, move in reverse migrations, or split into multiple populations. The different migrations of larvae, juveniles, and adults, suggest variations in migrations may be age-related (Brusca, 1967; Brinton, 1967; Fitch and Lavenberg, 1968; Pearcy et al., 1977, Willis and Pearcy, 1982; Eschmeyer et al., 1983). The divided populations, or "meso-bathypelagics" (Mackie and Mills, 1983, Mackie 1985), may be light-dependent, with the upper population responding to diel variations in light and the deeper group beyond the range of that stimulus.

The concept of a coherent "diel vertical migration" is a simplification, albeit useful, of a complex process. Diel migrations can vary by taxa, food, season, location, or biological state. Our understanding of many invertebrate taxa especially could benefit from further study, since current knowledge of many groups lacks the breadth and depth of fish research. A final understanding of the mechanisms and driving forces behind migrations may have to be determined by a species-by-species examination encompassing oceanography, biology, ecology, and ethology.

Submersible Observations

A good criterion of the utility of any sampling technique is whether both statistically meaningful counts and precise identifications can be obtained with relative ease (Harbison, 1983). Past studies have discussed the advantages and disadvantages of trawls (Table 14) and submersibles (Table 15), but without side-by-side detailed sampling. By reviewing submersible observations in complement with the intensive, concurrent trawling survey, the best aspects of each method become clearer.

There were some taxa abundant in both surveys. They were sturdy enough to survive trawl damage, and large enough to be readily identified in situ. All the animals had distinct coloration, with pink or red crustaceans and silvery fishes.

Multiple sampling techniques have often been useful in reducing technical constraints and compensating for biases of each type of gear (Clarke, 1977; Omori and Hamner, 1982). In this study, trawl and submersible data provided complementary insights into the fauna of the Monterey Submarine Canyon. The strengths and weaknesses of each method has been considered before, but these concurrent comparisons provided more details. The taxa most abundant in trawls were fishes and small, sturdy, semi-transparent taxa. The preliminary DEEP ROVER data identified fragile gelatinous animals and structures virtually absent in trawls. It also recorded small-scale phenomenon, including swarms and other types of patchiness, behavior, and multispecies associations. Inclusion of the video records will further enhance these details, and expand the number of taxa recorded from this method.

However, biases and limitations may remain. Since fishes avoid both trawls and submersibles, it is possible that deep pelagic fishes have not yet been completely and accurately sampled by either method or by both techniques combined.

In most ecological studies, researchers have begun with theories based on direct, qualitative observations and then moved into quantitative sampling and experimentation. Deep-sea biology has been studied in the reverse of this traditional order, beginning instead with indirect sampling and only most recently direct observation. Theories developed from trawls can at last be placed in their ecological context and tested by _in situ_ experimentation and observation (Robison and Wishner, 1990). Visual integration of the environment from submersible observations is added to the horizontal and vertical integration by trawls. Used separately or together, both methods are powerful and complementary tools for the understanding of the deep pelagic regions.

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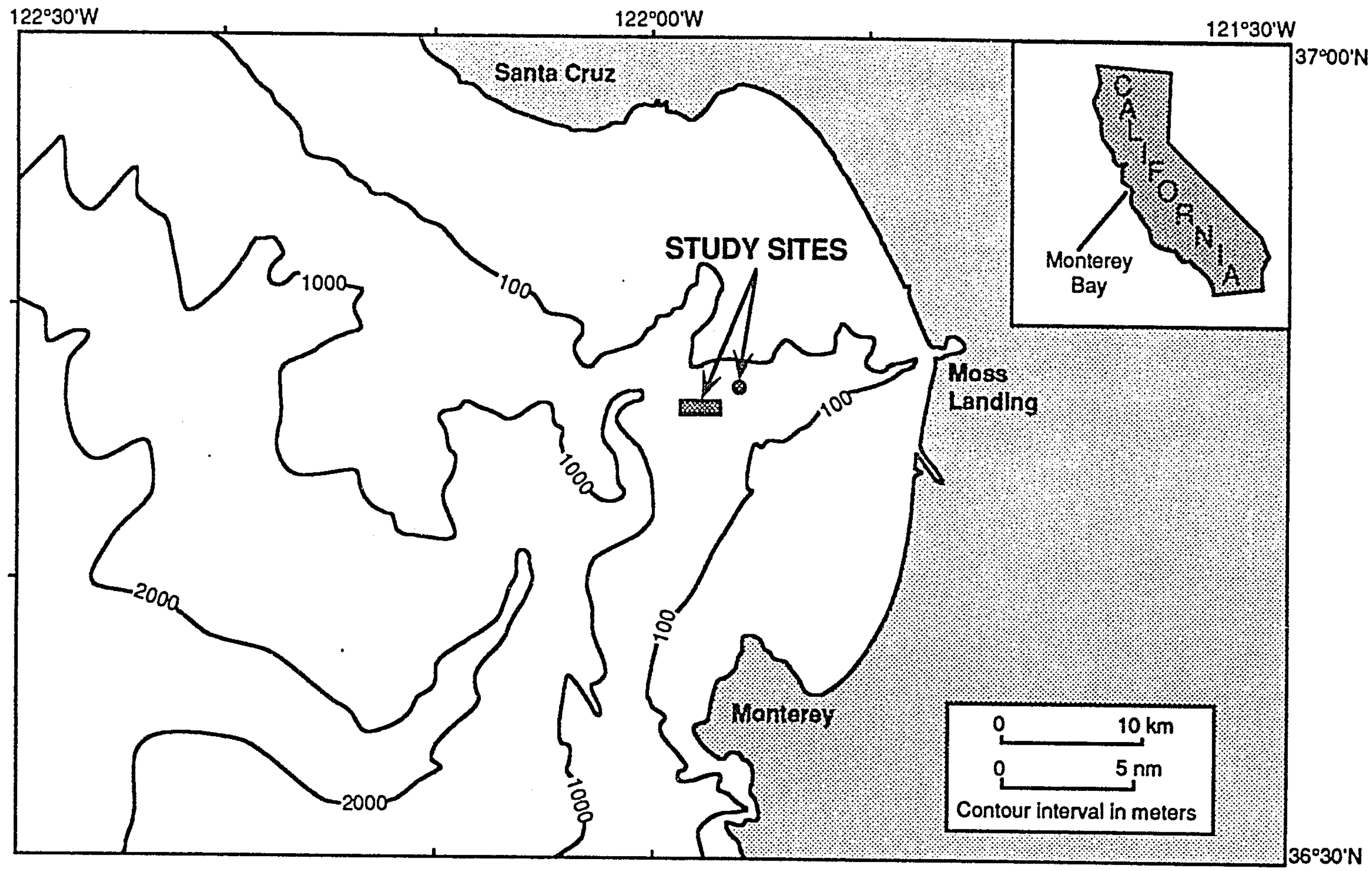


Figure 1. Map of the Monterey Submarine Canyon with trawl and submersible survey stations. Rectangle indicates trawl area, circle indicates DEEP ROVER dive site.

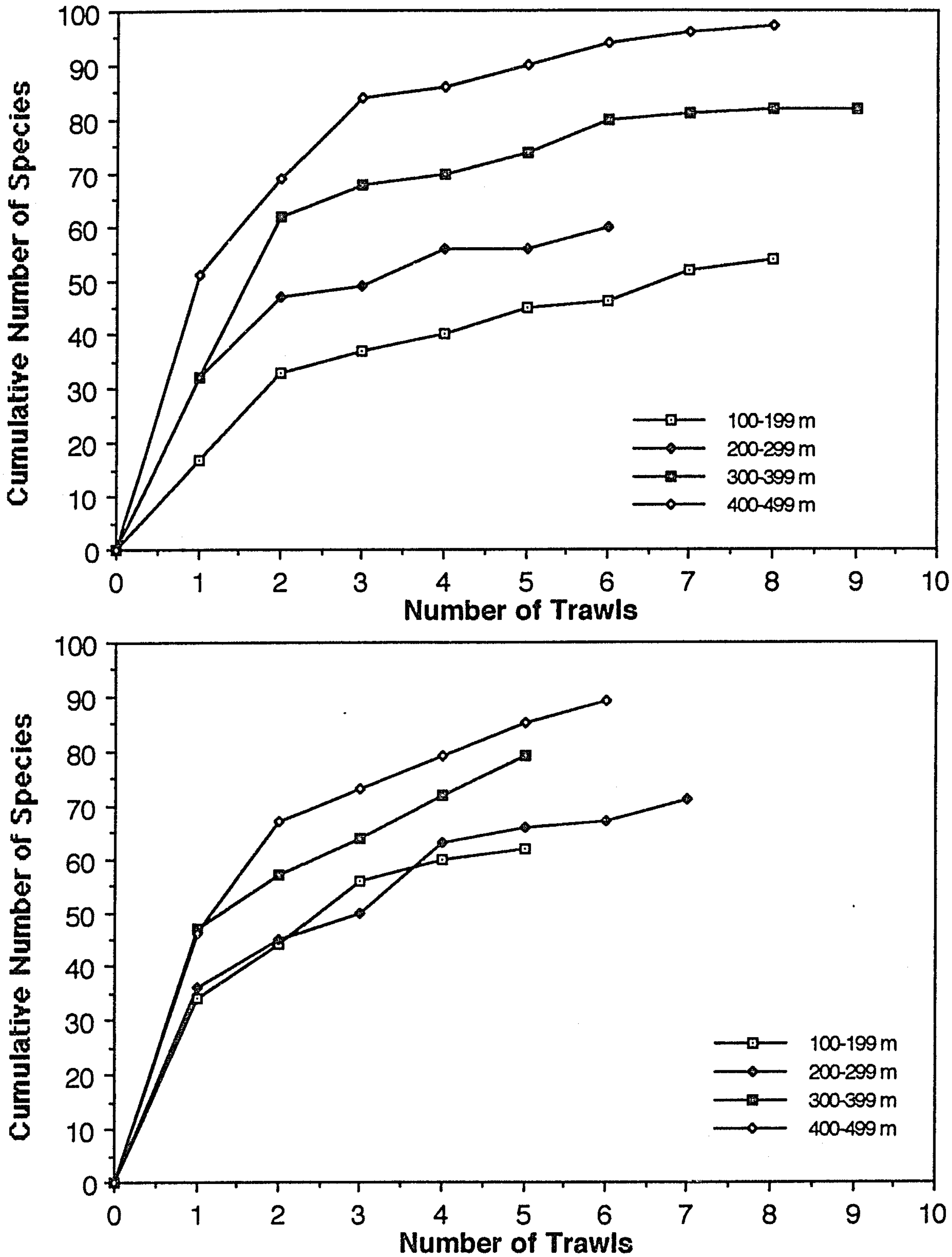


Figure 2. Cumulative total number of all taxa versus number of trawl samples for four 100-meter depth intervals by day trawls (upper) and night (lower).

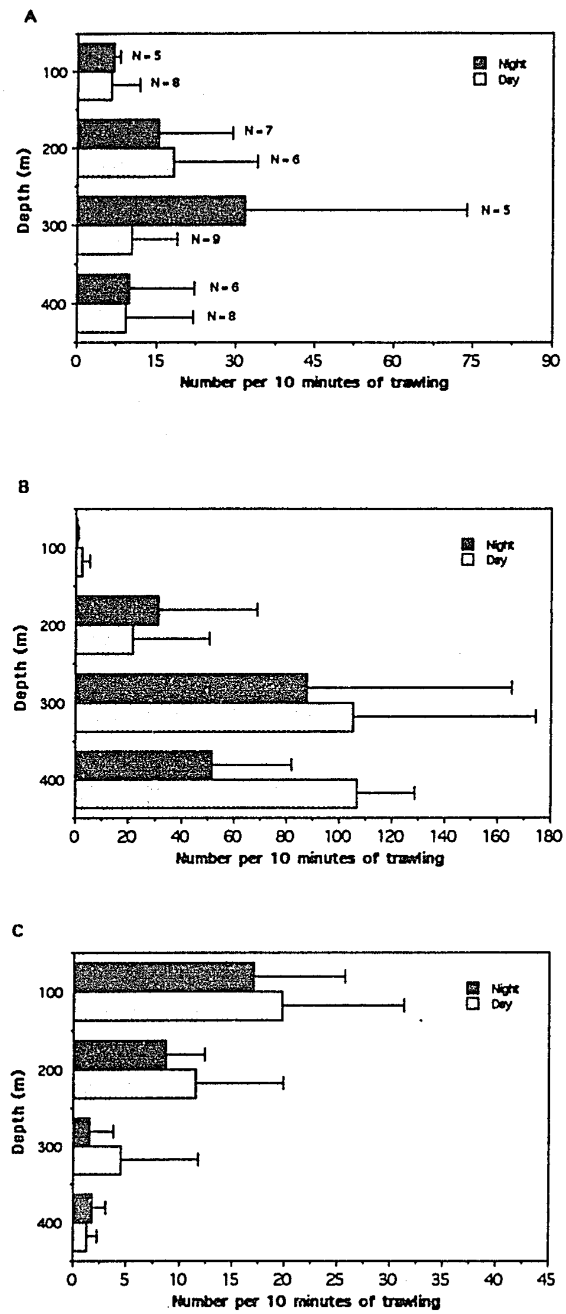


Figure 3. Mean abundances of selected cnidarians and ctenophores by depth intervals, day versus night. A. leptomedusans. Numbers indicate the quantity of trawls at that interval, B. calycophorans, C. Hormiphora californiensis. Note different horizontal scales. Light columns denote day, dark denote night. Bars indicate one standard error.

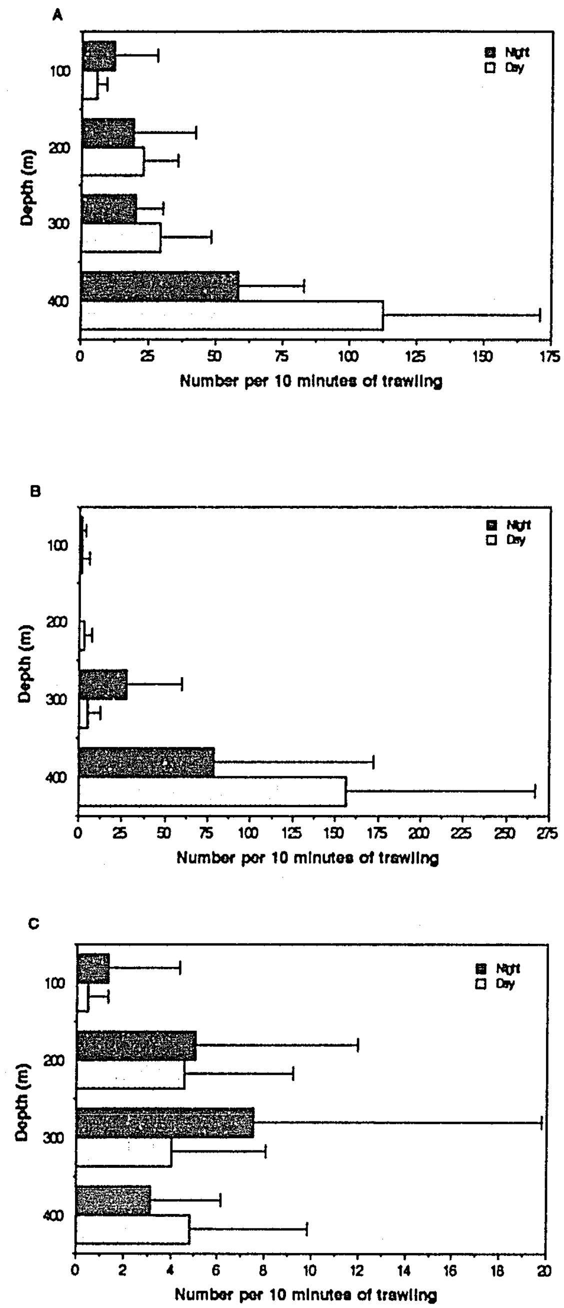


Figure 4. Mean abundances of selected copepods and mysids by depth intervals, day versus night. A. copepods, B. Boreomysis californica, C. Holmesiella anomala. Note different horizontal scales. Sample size and bars as in Figure 3.

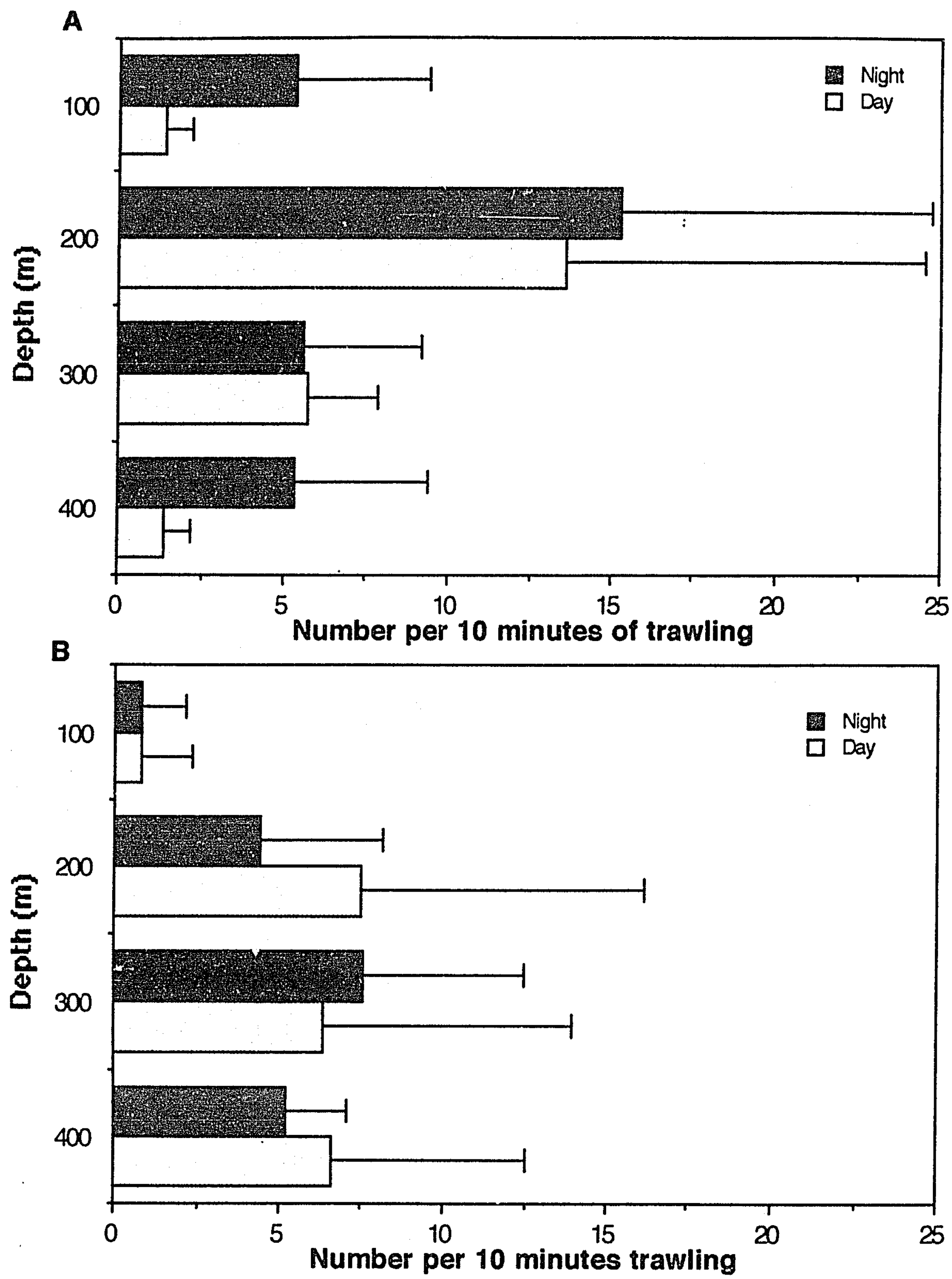


Figure 5. Mean abundances of selected amphipods by depth intervals, day versus night. A. Paraphronima spp., B. Orchomene spp. Sample size and bars as in Figure 3.

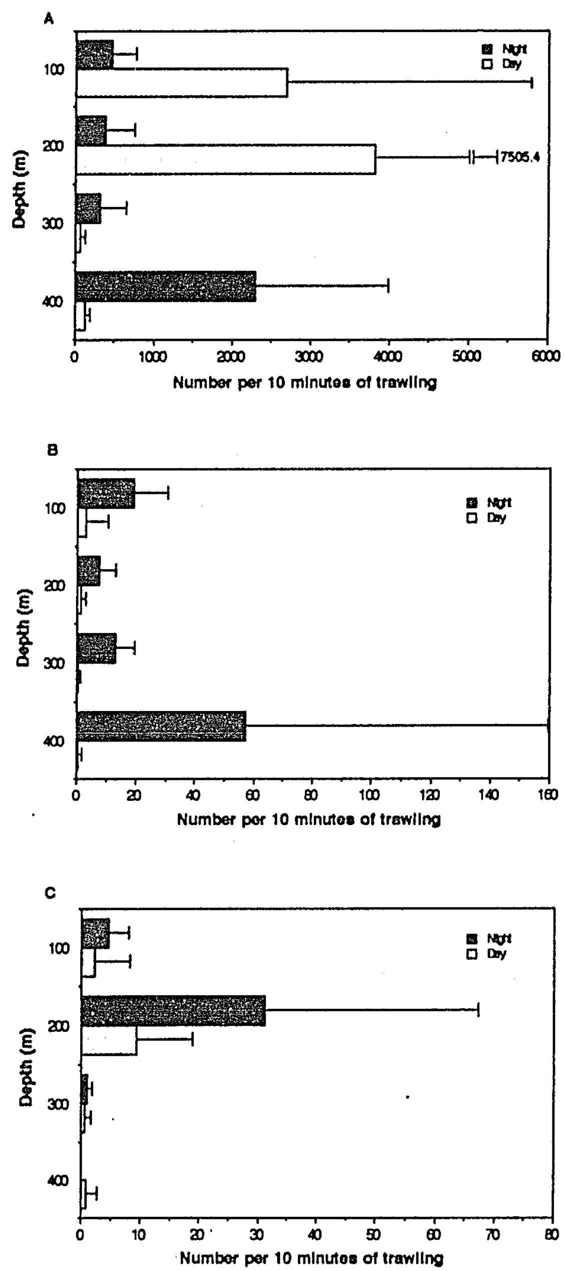


Figure 6. Mean abundances of selected euphausiids by depth intervals, day versus night. A. Euphausia pacifica, B. Thysanoessa spinifera, C. Nematoscelis difficilis. Note different horizontal scales. Sample size and bars as in Figure 3.

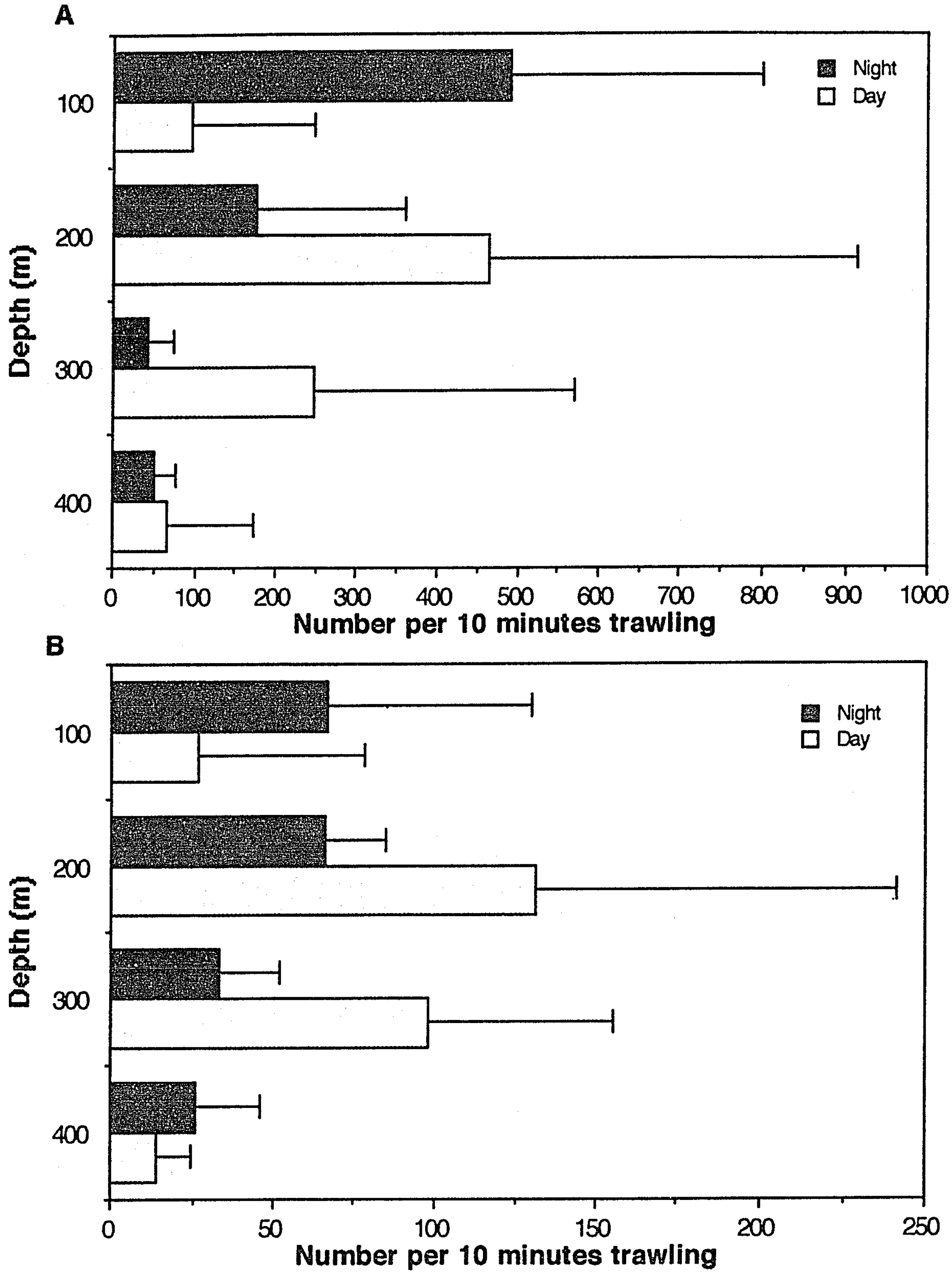
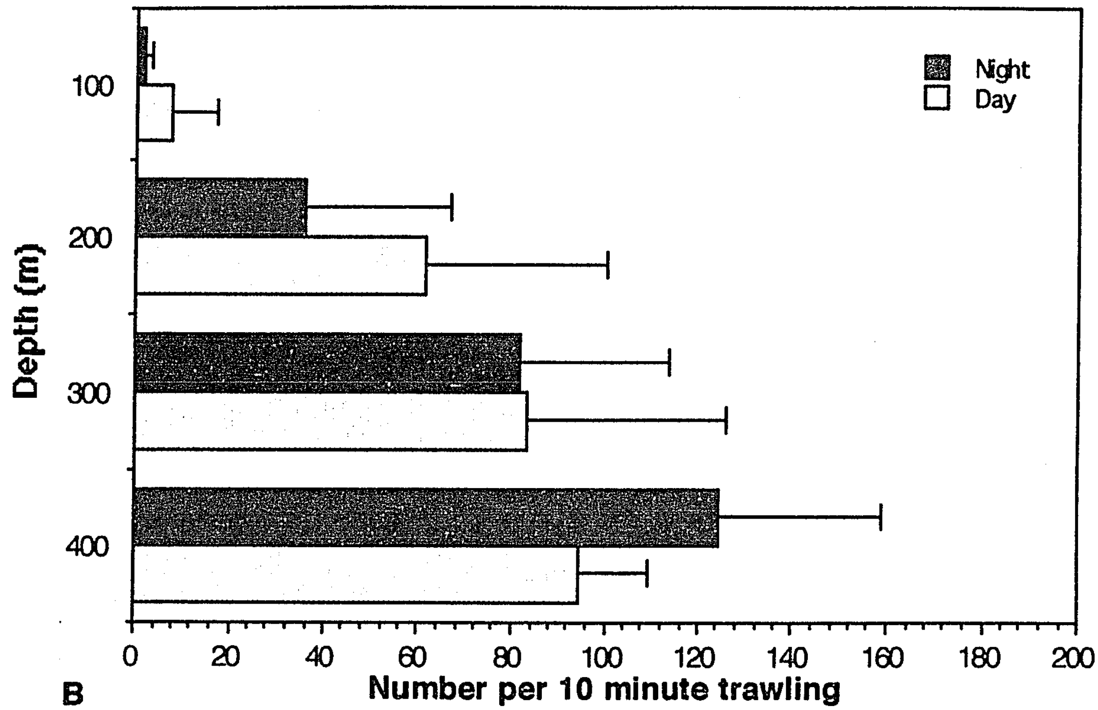


Figure 7. Mean abundances of selected natant decapods by depth intervals, day versus night. A. Sergestes similis, B. Pasiphaea pacifica. Note different horizontal scales. Sample size and bars as in Figure 3.

A



B

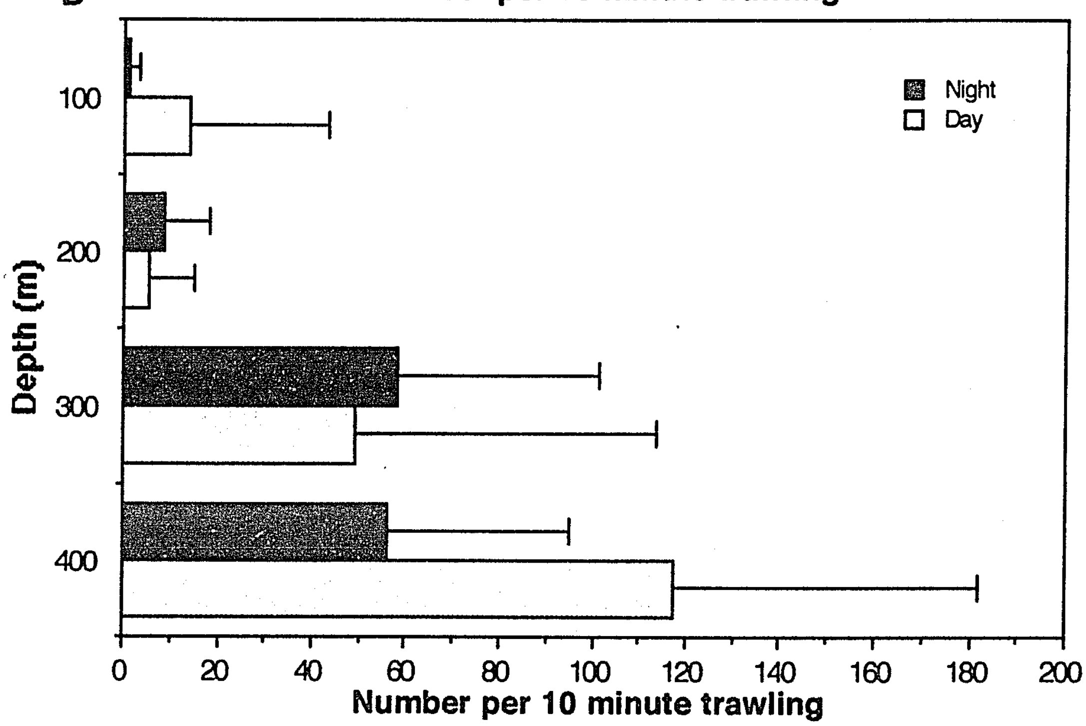


Figure 8. Mean abundances of chaetognaths and thaliaceans by depth intervals, day versus night. A. chaetognaths, B. Dolioletta gegenbauri. Sample size and bars as in Figure 3.

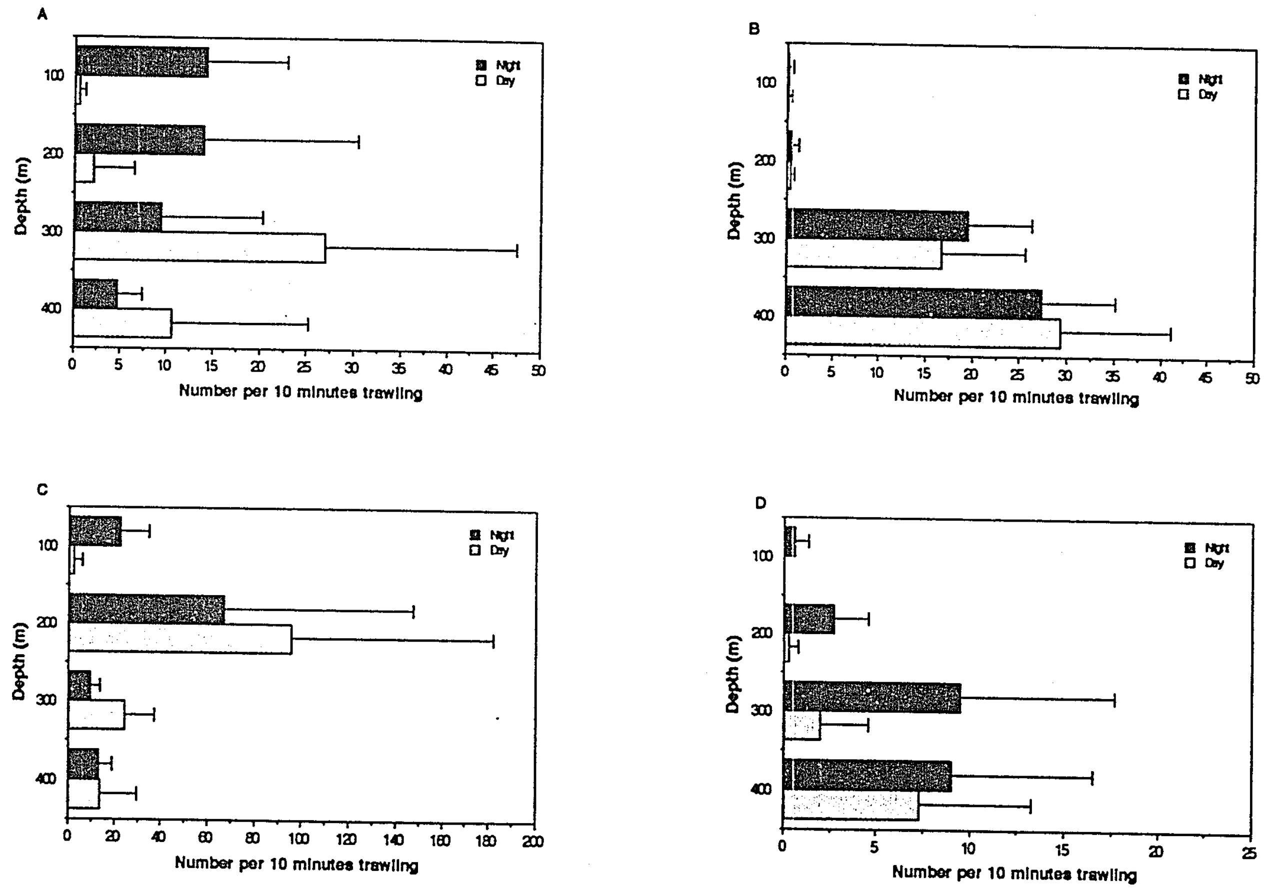
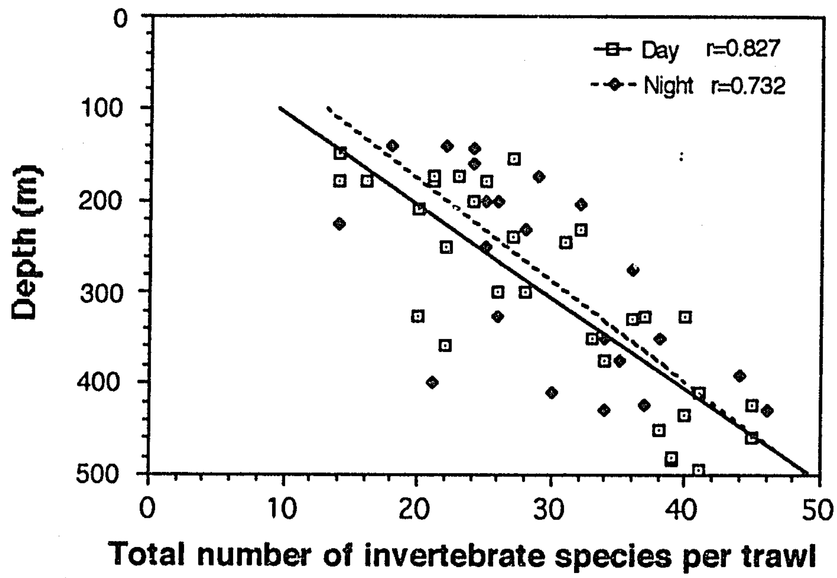


Figure 9. Mean abundances of selected fishes by depth intervals, day versus night. A. Leuroglossus stilbius, B. Cyclothone signata, C. Stenobrachius leucopsarus, D. Lycodapus mandibularis. Note different horizontal scales. Sample size and bars as in Figure 3.



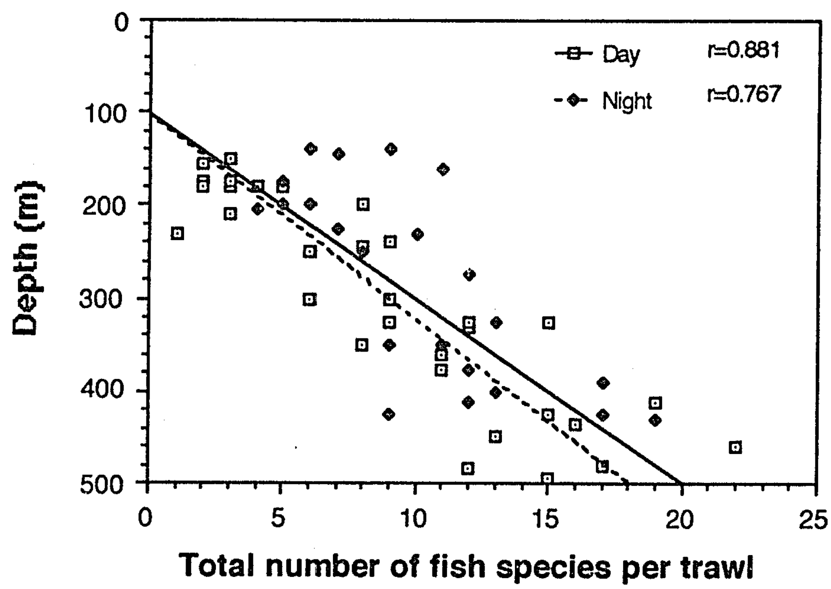
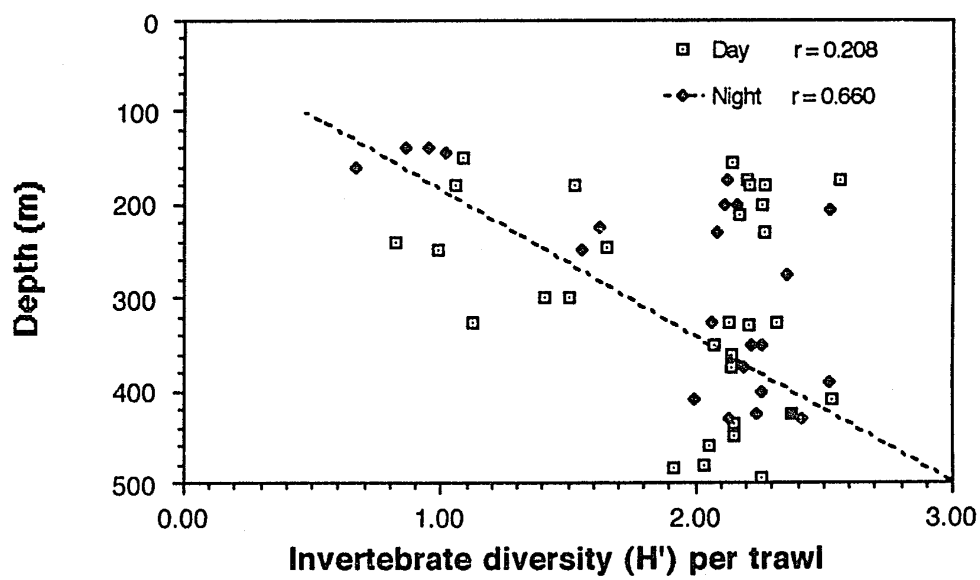


Figure 10. Relationship of the total number of species per trawl versus depth, for invertebrates (upper) and fishes (lower). Note different horizontal scales. Squares indicate day samples (N=31) and diamonds indicate night samples (N=24).



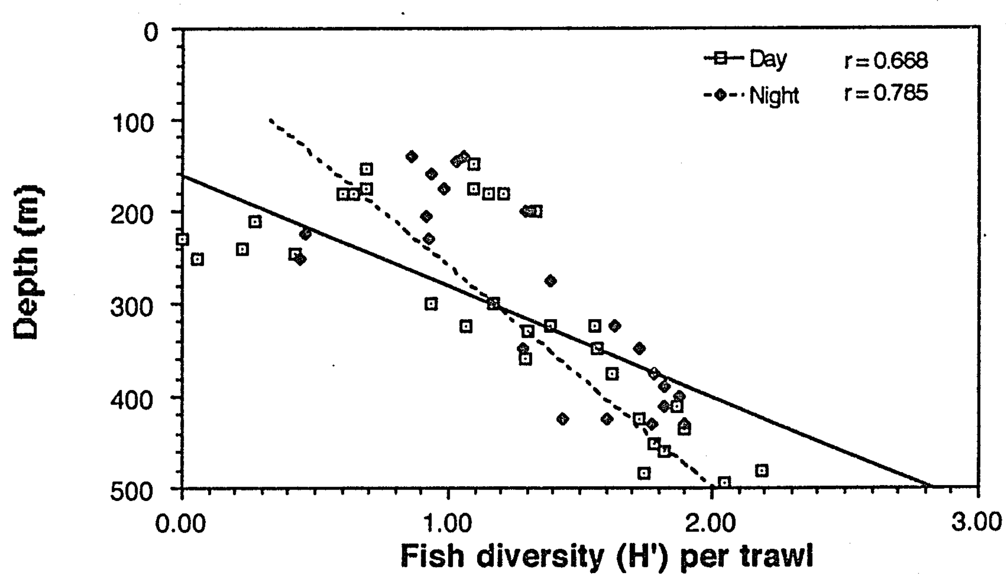


Figure 11. Relationship of the Shannon-Weiner diversity (H') versus depth, for invertebrates without Euphausia pacifica (upper) and fishes (lower). Sample size and symbols as in 10.

Table 1. Relative abundances of cnidarians and ctenophores by depth and time intervals. See below for abundance ratings

	DEPTH INTERVAL (100 m) DAY 100	200	300	400	NIGHT 100	200	300	400
PHYLUM CNIDARIA								
Class Hydrozoa								
Hydroida								
Anthomedusae								
Sarsia spp.	-	-	IF	IF	-	-	IF	IF
Euphysa spp.	-	IF	IF	IF	-	-	IF	-
Tiaranna spp.	-	-	-	C	-	-	IF	IF
Sibogita spp.	1	-	IF	-	-	1	-	1
Leptomedusae								
Leptomedusae unid.	C	A	C	C	C	A	A	A
Laodicea spp.	IF	-	C	C	1	IF	IF	C
Ptychogena spp.	C	C	C	C	IF	IF	IF	C
Trachymedusae								
Colobonema sericeum	1	-	C	C	IF	1	C	C
Crossota rufobrunnea	-	-	IF	1	-	-	-	-
Narcomedusae								
Aegina citrea	-	C	IF	IF	-	IF	IF	-
Coronomedusae								
Atolla wyvillei	-	-	C	C	-	-	C	C
Periphylla periphylla	-	-	IF	IF	1	-	IF	C
Siphonophora								
Calycophora								
Calycophora unid.	C	A	S	S	C	A	A	A
Physonectae								
Colonial siphonophora	IF	-	1	C	-	IF	IF	-
PHYLUM CTENOPHORA								
Hormiphora californiensis	A	A	C	C	A	C	IF	C
Beroe spp.	IF	IF	1	IF	-	IF	IF	-

1 = One specimen only.
IF = Infrequent; in 60% of the tows or less
C = Common; in more than 60% of the tows.
A = Abundant; mean number/10 minute 10-99.
S = Superabundant; mean number/10 minute 100-999.
SS = Superabundant; mean number/10 minute 1000 or greater.

Table 2. Relative abundances of molluscs by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Class Gastropoda								
Thecosomata								
Cavoliniidae								
<u>Clio pyramidata</u>	1	IF	-	1	1	-	1	-
Cymbulidae								
<u>Corolla spectabilis</u>	IF	C	C	C	C	IF	IF	IF
Gymnosomata								
Clionidae								
<u>Clione limacina</u>	C	C	C	C	C	C	C	C
Heteropoda								
<u>Carinaria japonica</u>	IF	IF	IF	IF	-	IF	IF	IF
Class Cephalopoda								
Decapoda								
Histeoteuthidae								
<u>Histeoteuthis heteropsis</u>	-	-	IF	-	-	IF	-	-
Octopoteuthidae								
<u>Octopoteuthis deletron</u>	-	-	-	-	1	-	-	-
Gonatidae								
Gonatus spp.	-	IF	IF	C	IF	C	IF	IF
Chiroteuthidae								
<u>Chiroteuthis calyx</u>	1	IF	-	IF	-	IF	1	1
Cranchiidae								
<u>Galiteuthis phyllura</u>	1	1	IF	IF	-	-	1	IF
Octopoda								
Bolitaenidae								
<u>Japetella heathi</u>	-	-	1	-	-	-	-	-
Octopodidae								
<u>Octopus</u> spp.	IF	1	IF	-	-	IF	-	IF

Table 3. Relative abundances of annelids by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Polychaeta								
Tomopteris spp.	IF	C	C	C	IF	IF	IF	IF
Poeobius meseres	-	-	IF	IF	-	1	IF	IF
Aphrodita spp.	-	-	IF	IF	1	IF	-	-

Table 4. Relative abundances of crustaceans: ostracods, copepods, and mysids by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Ostracoda								
Ostracoda unidentified	IF	IF	IF	C	IF	IF	IF	1
Copepoda								
Copepoda unidentified	C	A	A	S	A	A	A	A
Gaussia princeps	IF	1	-	C	-	-	-	IF
Malacostraca								
Mysidacea								
Eucopia spp.	-	-	1	IF	-		IF	1
Boreomysis californica	IF	IF	C	S	IF	IF	A	A
Holmesiella anomala	IF	C	C	C	IF	IF	C	C

Table 5. Relative abundances of crustaceans: amphipods by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Hyperiidea								
Mimonectidae								
Mimonectes spp.	-	-	-	IF	-	-	-	-
Scinidae								
Scina spp.	1	-	IF	C	1	IF	C	C
Lanceolidae								
Lanceola loveni	-	-	-	1	-	-	-	-
Vibiliidae								
Vibilia spp.	IF	IF	IF	IF	1	IF	C	IF
Cystisomatidae								
Cystisoma fabricii	-	-	1	IF	IF	IF	C	C
Paraphronimidae								
Paraphronima spp.	A	A	C	C	C	A	C	C
Hyperiidae								
Hyperia medusarum	IF	C	C	C	IF	C	C	C
Hyperoche medusarum	IF	IF	IF	C	IF	IF	IF	C
Parathemisto pacifica	IF	IF	IF	IF	IF	IF	IF	C
Phronimidae								
Phronima spp.	C	C	C	C	C	C	C	IF
Phrosinidae								
Primno macropa	IF	IF	C	C	-	IF	C	C
Primno brevidens	C	C	IF	C	IF	C	IF	IF
Pronoidae								
Euprone minuta	1	-	-	1	-	-	-	IF
Lycaeidae								
Lycaea spp.	-	-	-	-	-	-	-	1
Oxycephalidae								
Streetsia challengeri	IF	C	IF	IF	C	C	1	IF
Gammaridea								
Eusiridae								
Cleonardo spp.	-	-	-	IF	-	-	-	1
Hyperiopsidae								
Hyperiopsis spp.	-	-	-	IF	-	-	1	1
Lysianassidae								
Cyphocaris anonyx	-	-	-	1	-	-	-	IF
Cyphocaris richardi	-	-	-	1	-	-	-	-
Orchomene spp.	IF	C	C	C	IF	C	C	C
Valettiopsis spp.	-	-	-	1	-	-	-	-
Stegocephalidae								
Paracallisoma alberti	-	-	-	1	-	-	-	-
Parandania boecki	-	-	-	1	-	-	-	-
Stilipedae								
Stilipes distincta	-	-	IF	C	-	-	IF	C

Table 6. Relative abundances of crustaceans: eucarids and decapods by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Eucarida								
Euphausiacea								
Euphausia pacifica	SS	SS	A	S	S	S	S	SS
Nematoscelis difficilis	IF	C	IF	IF	C	A	C	-
Thysanoessa spinifera	IF	IF	IF	IF	A	C	A	A
Nematobrachion flexipes	-	-	-	-	-	1	1	-
Decapoda								
Peneides								
Sergestes similis	A	S	S	A	S	S	A	A
Gennadas propinquus	-	-	IF	IF	-	IF	-	IF
Carides								
Pasiphaea pacifica	A	S	A	A	A	A	A	A
Pandalus jordani	-	IF	IF	1	IF	IF	-	-
Hippolytidae	-	-	1	-	-	1	-	-
Decapod larvae	C	C	C	C	C	C	IF	IF

Table 7. Relative abundances of chaetognaths and thaliacians by depth and time intervals. Ag. = aggregate life history phase, sol. = solitary phase, total = total abundance of all phases. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
PHYLUM CHAETOGNATHA								
Chaetognatha unid.	C	A	A	A	C	A	A	S
PHYLUM CHORDATA								
Thaliacea								
Salpidae								
Salpa fusiformis (agg.)	IF	IF	IF	IF	IF	C	IF	IF
S. fusiformis (sol.)	IF	IF	IF	IF	1	IF	IF	-
S. fusiformis (total)	IF	IF	IF	IF	IF	C	IF	IF
Thalia democratica (agg.)	1	IF	IF	IF	-	IF	-	IF
T. democratica (sol.)	-	IF	1	-	IF	IF	-	1
T. democratica (total)	1	IF	IF	IF	IF	IF	-	IF
Iasis zonaria (sol.)	-	IF	-	-	1	-	-	-
Cyclosalpa spp.	-	-	-	-	1	-	-	-
Doliolidae								
Dolioletta gegenbauri	C	IF	IF	A	IF	IF	IF	C
D. gegenbauri (nurse)	C	C	A	A	IF	C	A	A
D. gegenbauri (total)	A	C	A	A	C	C	A	A
Gelatinous case	1	IF	IF	1	-	IF	-	-

Table 8. Relative abundances of large (> 1/2 m TL) fishes by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Class Cephalaspidomorphi								
Petromyzontidae								
Lampetra tridentata	-	1	-	-	-	-	-	-
Class Elasmobranchiomorphi								
Scyliorhinidae								
Parmaturus xaniurus	-	-	-	1	-	-	-	1
Apristurus brunneus	-	-	-	-	-	-	-	R
Squalidae								
Somniosus pacificus	-	-	-	-	-	1	-	-
Class Osteichthys								
Icosteidae								
Icosteus aenigmaticus	-	-	-	1	-	-	-	-

Table 9. Relative abundances of larval and juvenile fishes by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Clupeidae (juvenile)								
Clupea harengus pallisi	-	-	-	-	-	1	-	-
Engraulidae (juvenile)								
Engraulis mordax	-	-	-	-	-	1	R	1
Platytroctidae (juvenile)								
Sagamichthys abei	-	-	R	R	-	-	1	R
Bythitidae (juvenile)								
Cataetyx rubrirostris	-	1	-	-	-	-	1	1
Scomberesocidae (juvenile)								
Cololabis saira	-	-	-	-	-	1	-	-
Trachipteridae (juvenile)								
Trachipterus altivelis	-	-	-	-	-	-	-	1
Scorpaenidae (juvenile)								
Sebastes spp.	1	R	1	R	C	R	1	R
Sebastolobus spp.	-	-	-	R	R	-	-	-
Agonidae (juvenile)								
Occella verrucosa	-	-	1	-	-	-	-	-
Stichaeidae (juvenile)								
Plectobranchus evides	-	1	-	-	R	-	-	-
Centrolophidae (juvenile)								
Icichthys lockingtoni	-	-	-	-	1	-	1	-
Bothidae (larvae)								
Citharichthys stigmaeus	1	1	1	1	R	-	1	R
Citharichthys sordidus	-	-	-	-	R	R	-	1
Citharichthys spp. (total)	R	C	R	R	C	R	R	R
Pleuronectidae (larvae)								
Errex zachirus	R	R	C	C	C	R	R	R
Eopsetta exilis	R	R	R	-	-	-	-	-
Microstomus pacificus	-	-	1	-	-	-	1	1

Table 10. Relative abundance of fishes by depth and time intervals. See Table 1 for explanation of abundance ratings.

	DEPTH INTERVAL (100 m)							
	DAY				NIGHT			
	100	200	300	400	100	200	300	400
Argentinidae								
<u>Argentina</u> <u>sialis</u>	1	-	-	-	1	-	-	1
Bathylagidae								
<u>Leuroglossus</u> <u>stilbius</u>	C	C	A	A	A	A	C	C
<u>Bathylagus</u> <u>ochotensis</u>	-	-	-	C	-	-	-	-
<u>Bathylagus</u> <u>wesethi</u>	-	-	-	IF	-	-	-	-
Gonostomatidae								
<u>Cyclothone</u> <u>signata</u>	IF	IF	A	A	IF	IF	A	A
<u>Cyclothone</u> <u>acclinidens</u>	-	-	-	C	-	IF	-	IF
<u>Cyclothone</u> <u>pacifica</u>	-	1	-	IF	-	-	-	IF
<u>Cyclothone</u> <u>pseudopallida</u>	-	-	IF	C	-	-	IF	C
Sternoptychidae								
<u>Sternoptyx</u> spp.	-	-	-	IF	-	-	-	1
<u>Sternoptyx</u> <u>pseudobscura</u>	-	-	-	1	-	-	-	-
<u>Argyropelecus</u> <u>affinis</u>	-	-	1	-	-	-	-	-
<u>Argyropelecus</u> <u>sladeni</u>	-	-	IF	1	-	-	1	IF
<u>Danaphos</u> <u>oculatus</u>	-	-	1	1	-	-	-	-
Chauliodontidae								
<u>Chauliodus</u> <u>macouni</u>	-	-	IF	C	1	1	IF	C
Melanostomiatidae								
<u>Tactostoma</u> <u>macropus</u>	-	-	-	-	-	-	-	IF
Idiacanthidae								
<u>Idiacanthus</u> <u>antrostomus</u>	-	-	IF	IF	-	-	IF	C
Myctophidae								
<u>Stenobrachius</u> <u>leucopsarus</u>	IF	A	A	A	A	A	A	A
<u>Lampanyctus</u> <u>ritteri</u>	-	1	C	C	IF	IF	C	C
<u>Lampanyctus</u> <u>regalis</u>	-	-	1	1	1	-	1	IF
<u>Tarletonbeania</u> <u>crenularis</u>	-	IF	IF	C	IF	IF	C	C
<u>Protomyctophum</u> <u>crockeri</u>	IF	-	IF	C	IF	IF	IF	IF
<u>Diaphus</u> <u>theta</u>	-	IF	1	IF	-	IF	-	-
<u>Diogenichthys</u> <u>atlanticus</u>	-	-	-	1	-	-	IF	-
Neoscopelidae								
<u>Scopelengys</u> <u>tristis</u>	-	-	-	IF	-	-	-	-
Merlucciidae								
<u>Merluccius</u> <u>productus</u>	-	IF	-	IF	IF	IF	-	IF
Zoarcidae								
<u>Lycodapus</u> <u>mandibularis</u>	-	IF	IF	C	IF	C	C	C
<u>Melanostigma</u> <u>pammelas</u>	-	-	-	C	-	-	IF	IF
Cyclopteridae								
<u>Nectoliparis</u> <u>pelagicus</u>	-	-	C	C	IF	C	C	C
<u>Lipariscus</u> <u>nanus</u>	-	-	IF	IF	-	-	IF	IF

Table 11. Percent similarity indices, day versus night. A. Total invertebrates, B. All invertebrates except dominant Euphausia pacifica, C. fishes.

A. Total invertebrates

		DAY			
	Depth (m)	100-199	200-299	300-399	400-499
NIGHT	100-199	48.6	88.9	15.2	20.4
	200-299	75.2	63.5	24.9	26.9
	300-399	56.4	68.5	56.5	57.3
	400-499	49.0	60.4	60.8	31.5

B. Invertebrates without dominant euphausiid

		DAY			
	Depth (m)	100-199	200-299	300-399	400-499
NIGHT	100-199	64.5	73.7	68.5	30.0
	200-299	60.0	79.0	71.5	29.6
	300-399	25.6	48.9	64.5	55.8
	400-499	22.3	43.1	72.6	74.5

C. Fishes

		DAY			
	Depth (m)	100-199	200-299	300-399	400-499
NIGHT	100-199	68.9	57.8	51.7	36.7
	200-299	75.6	80.2	36.0	20.9
	300-399	38.1	38.9	64.9	61.7
	400-499	32.2	33.8	83.8	84.1

Table 12. Shallowest depth in meters of occurrence of comparable species collected by trawl and submersible.

Species	First Appearance: Trawl	First Appearance: Submersible
Periphylla periphylla	145	371
Colobonema sericeum	145	244
narcomedusae	230	198
physonect siphonophore	155	137
calycophorid siphonophore	155	152
Beroe spp.	175	131
Hormiphora californiensis	150	134
pteropod	150	349
heteropod	175	131
octopod	155	131
squid	140	144
Poeobius meseres	205	394
copepod	140	137
amphipod	140	150
euphausiid	140	134
Pasiphaea pacifica	140	144
Sergestes similis	140	122
chaetognath	140	137
salp	140	197
doliolid	140	616
cat shark	410	464
larval fish	140	137
larval flatfish	140	134
Leuroglossus stilbius	140	137
bathylagid	410	686
Cyclothone spp.	160	396
Chauliodus macouni	145	533
Idiacanthus antrostomus	325	557
Stenobrachius leucopsarus	140	131
Diaphus theta	240	381
Tarletonbeania crenularis	245	564
Lampanyctus spp.	140	584
Merluccius productus	160	134
Melanostigma pammelas	390	195
Lycodapus mandibularis	140	274
liparid (cyclopterid)	140	533

Table 13. Most common taxa collected by midwater trawl and R/S DEEP ROVER, ranked by frequency of occurrence.

TRAWL	DEEP ROVER
Euphausia pacifica	Nanomia bijuga
Sergestes similis	Merluccius productus
Pasiphaea pacifica	Leuroglossus stilbius
calycophorid siphonophore	Pasiphaea pacifica
chaetognath	Sergestes similis
Dolioletta gegenbauri	Apolemia sp.
copepod	lobate ctenophore
Stenobrachius leucopsarus	Stenobrachius leucopsarus
Cyclothone spp.	euphausiid
Leuroglossus stilbius	ctenophore

Table 14. Summary of advantages and disadvantages of using trawls for midwater surveys as determined from this and other studies.

ADVANTAGES	OTHER STUDIES
Large areas and water volumes are sampled, making it a good medium-scale survey technique	Mauchline, 1970; Mauchline, 1977; Madin, 1990
Large numbers of specimens for research	Mauchline, 1970
Able to collect data on biomass of fauna	e. g. Ebeling et al., 1970
Extensive data base for some taxa	Mauchline, 1977
Certain rarer species collected	Mauchline, 1970
Collects small, sturdy fauna	
Less costly and technologically dependant than submersible	Robison, 1983

DISADVANTAGES	
Sampling indirect	Harbison, 1983; Robison, 1983; Madin, 1990
Vertical movement of trawl up to 20 m	Robison, 1983
Animals from a large area combined into one sample	Harbison, 1983;Robison, 1983
Avoidance by large, fast animals including migrators	e. g. Barham, 1963, 1966; McGowan and Fraundorf, 1966; Pearcy and Laurs, 1966; Harrisson, 1967; Barham, 1970; Robison, 1983; Mackie, 1985 and others
Animals escape through trawl mesh	Barham, 1966; Robison, 1983
Fragile structures and animals, especially ctenophores, destroyed	Barham, 1966; Robison, 1983

Table 15. Summary of advantages and disadvantages of submersibles for midwater surveys as determined from this and other studies.

ADVANTAGES	OTHER STUDIES
In situ observation and manipulation, with real-time response to new data possible	Mackie and Mills, 1983; Alldredge et al., 1984; Widder et al. 1989; Madin, 1990
Sampling of areas to steep, narrow, or rocky for trawls	Saunders, 1972
Migrations, patchiness, ethology, biology, and physical parameters can be studied quantitatively in situ	Barham, 1970; Mackie and Mills, 1983; Robison, 1983; Alldredge et al., 1984; Vinogradov et al., 1985; Mills, 1987; Madin, 1990; Robison and Wishner, 1990
Live undamaged damaged specimens, especially of fragile gelatinous taxa are now available for study	Barham, 1963; Omori and Hamner, 1982; Harbison, 1983; Robison; 1983; Hamner, 1985; Madin, 1990; Etchmendy and Davis, 1991
Assumptions about diversity, abundance, and avoidance based on trawl data are being reviewed and revised	Robison, 1983

DISADVANTAGES	
Recognition of species difficult, especially for small species	Harbison, 1983; Robison, 1983
Expertise of viewers critical to amount of data collected	Mauchline, 1977; Mackie and Mills, 1983
Quantification of transects difficult	Robison, 1983
Attraction and contamination of depth transects by some species	Mackie and Mills, 1983
Avoidance by mesopelagic fishes	Robison, 1983
Costly and dependent on weather and delicate technology	Robison, 1983
Design limitations on visibility, mobility and duration of transects	Robison, 1983

Appendix 1. Trawl Data of Deep Rover Assessment Group, 3 - 11 September 1985.

Date	Tow #	Deployment: Net Open	Deployment: Net Close	Depth (m)	Lat. 36º N	Long. 121º W	Min bottom depth	In Deep Scattering Layer?
3	1	1000	1030	300	46.7	57.9	600	Y
3	2	1241	1301	150	46.6	58.6	600	N
3	3	1507	1531	325	46.5	58.3	820	Y
3	4	1751	1819	200	46.6	58.7	220	Y
3	5	2118	2135	375	46.5	57.1	730	Y
3	6	2324	2344	205	46.5	58.0	590	Y
4	7	0140	0205	350	46.8	57.8	420	Y
4	8	0853	0919	350	46.6	57.6	570	Y
4	9	1108	1123	375	46.0	57.6	550	Y
4	10	TDR failure		-	46.7	57.9	-	-
4	11	1715	1732	457	46.6	58.1	570	N
4	12	2030	2101	355	46.6	57.8	600	Y
4	13	2249	2319	205	46.7	57.8	600	N
5	14	0054	0124	205	46.7	57.8	550	Y
5	15	1014	1044	180	46.6	58.1	530	N
5	16	TDR failure		-	46.6	57.5	-	-
5	17	1444	1514	325	46.7	57.4	550	N
5	18	1717	1735	180	46.5	58.1	600	Y
5	19	2027	2057	175	46.7	57.2	640	N
5	20	2218	2248	275	46.6	57.7	600	Y
6	21	0053	0123	250	46.7	57.5	550	Y
6	22	0755	0826	180	46.8	57.9	540	Y
6	23	0951	1024	330	46.7	57.7	570	Y
6	24	1225	1258	245	46.8	57.3	570	N
6	25	1428	1500	410	46.7	57.6	550	Y
6	26	TDR failure		-	46.6	-	-	-
6	27	2247	2317	425	46.6	57.6	620	Y
7	28	0046	0114	145	46.6	57.3	570	Y
7	29	0813	0841	210	47.0	56.6	530	Y
7	30	1106	1132	460	46.7	57.6	590	Y
7	31	1346	1412	240	46.6	57.7	550	N
7	32	1617	1644	495	46.6	57.6	640	N
7	33	2118	2142	430	46.6	57.9	750	Y
7	34	2352	2421	325	46.6	57.7	550	Y
8	35	0202	0233	160	46.6	57.9	570	Y
8	36	0852	0916	435	46.8	58.0	460	Y
8	37	1341	1407	300	46.6	57.6	570	Y
8	38	1549	1618	360	46.6	57.6	590	Y

Appendix 1. (cont.)

Date	Tow #	Deployment: Net Open	Close	Depth (m)	Lat. 36° N	Long. 121° W	Min bottom depth	In Deep Scattering Layer?
8	39	1828	1855	425	46.7	57.4	550	Y
8	40	2115	2128	410	46.6	58.1	550	Y
8	41	2344	0017	140	46.5	58.0	590	Y
9	42	0213	0245	390	46.7	57.9	530	N
9	43	TDR failure		-	46.3	57.5	-	-
9	44	1113	1141	175	46.8	57.5	530	Y
9	45	1354	1412	480	46.8	56.9	550	N
9	46	1540	1619	250	46.6	57.5	620	Y
9	47	To DEEP ROVER		team	46.3	57.5	-	-
9	48	2340	0011	225	46.6	57.1	690	Y
10	49	0148	0204	400	46.7	57.9	530	Y
10	50	0803	0825	230	46.1	57.7	600	Y
10	51	1003	1032	325	46.6	57.6	600	Y
10	52	1230	1302	180	46.7	58.0	550	N
10	53	1441	1509	485	46.2	57.9	650	N
10	54	2047	2120	425	46.2	57.6	610	N
10	55	2323	2358	430	46.3	57.7	700	N
11	56	0150	0218	230	46.5	57.9	600	Y
11	57	0328	0359	140	46.7	57.8	550	Y
11	58	0839	0907	155	46.9	58.9	450	N
11	59	1054	1122	175	46.9	57.8	550	Y
11	60	To DEEP ROVER		team	-	-	-	-